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嵩草属植物的胚胎学*

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摘要：对嵩草属（*Kobresia*）植物进行了初步的胚胎学研究。该属植物具假四合花粉（pseudomonad）；药室内壁在二核花粉时期开始螺旋状加厚，花药表皮在花粉成熟时形成乳突；成熟花粉具三细胞。胚珠为倒生型，具厚珠心和双层珠被，珠孔由内珠被构成，珠柄的近基部向珠孔增生形成珠孔塞。胚囊的发育为蓼型，四分体线形排列，合点端大孢子发育成八核胚囊。受精后，胚乳核先于受精卵进行分裂，胚乳的发育为核型。胚的发育为柳叶菜型灯芯草变型。通过比较，嵩草属植物大小孢子的发育、胚珠的结构、胚囊的发育、胚乳的发育和胚的发育与莎草科中其它类群一致。所以，根据胚胎学资料，嵩草属及其近缘属应保留在莎草科中，不该另立为嵩草科。

关键词 嵩草属，胚胎学，系统位置
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The Embryology of the Genus *Kobresia* (Cyperaceae)

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Abstract: The embryology of *Kobresia* was studied preliminarily. The development of megaspore and microspore, as well as the structure of ovule, is identical to that of other groups in Cyperaceae. The pollen of the genus is pseudomonad, the embryo sac is of *Polygonum* type, the endosperm is of nuclear type, and the embryogeny is of the Juncus variation of Onagrad type. These embryological characters are agreeable with those of the Cyperaceae. Therefore, the genus *Kobresia* and its related genera (*Carex*, *Schoenoxiphium* and *Uncinia*) should be retained in the family Cyperaceae other than raised as a separate family, Kobresiaceae.

Key words: *Kobresia*; Embryology; Systematic relationship

Kobresia Willdenow, a mainly Northern Hemisphere genus, belongs to the tribe Cariceae of the family Cyperaceae. Based on its morphology, especially the inflorescence morphology, the tribe Cariceae was once separated from Cyperaceae and proposed as a new family, Kobresiaceae (Gilly, 1952). The Kobresiaceae has not been accepted by other cyperologists since it was proposed. In the new classification of the Cyperaceae by Bruhl (1995) the tribe was included in the family. Moreover, the anatomical evidence does not support the establishment of the new family (Metcalf, 1971). The

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analysis of rbcL sequences shows the family Cyperaceae as monophyletic and derived from a juncaceous grade (Muasya *et al* , 1998).

The genus *Kobresia* is poorly understood in many respects, and even devoid of the embryological data. However, the embryological data provide numerous helpful evidences for systematic studies in Cyperaceae as well as the Juncales (Linder & Kellogg, 1995; Munro & Linder, 1997). Therefore, the embryology of *Kobresia curvata* (Boott ex C. B. Clarke) Kükenthal and *K. filicina* C. B. Clarke is studied preliminarily, and its implications for the systematic relationships of both *Kobresia* and the Cariceae are discussed.

1 Materials and Methods

The materials for embryological study were field - collected and preserved in FAA. Two species were studied: 1. *K. curvata* (Boott ex C. B. Clarke) Kükenthal: China, Xizang, Yadong, 3400 m, 1996 - 06 - 05, Lou Y B & Zhang S R 69 (voucher at PE); 2. *K. filicina* C. B. Clarke: China: Yunnan, Lijiang, 3000 ~ 3050 m, 1996 - 08 - 02, Zhang S R 71 (voucher at PE). The embryogeny and the endosperm formation of the first species, and the anther, microspores, ovule, megaspore mother cell and development of embryo sac of the second species were observed. The transverse sections of male flowers and the longitudinal sections of female spikelets were made through the usual paraffin method, stained with safranine and fast green.

2 Results

2.1 Anther and Microspores

The anther is tetrasporangiate (pl. Ⅰ :1). The formation of anther wall is unseen. At early 2 - nucleate stage of pollen grains, middle layer has disappeared, The wall of microsporangium comprises a single - layered epidermis, endothecium, and degenerated and vestigial tapetum (pl. Ⅰ :1 ~ 2). At maturity, the epidermis cells become papillate (pl. Ⅰ :5), and the endothecium develops spiral thickenings (pl. Ⅰ :3 ~ 5).

The primary sporogenous cells, microspore mother cells and meiosis have not been observed. After meiosis, one microspore nucleus of tetrad develops; other three are pushed towards the tapering end of the microspore mother cell. The former is functional microspore nucleus while the others are non - functional and degenerate later. At early 2 - nucleate stage, the vestiges of the three degenerated microspores are still visible (pl. Ⅰ :2 ~ 3). At this time, a few folds of wall are observed, and vacuole begins to develop (pl. Ⅰ :3). With the vacuole increasing in size, the folds vanish; a larger vegetative nucleus and a smaller generative nucleus are observed (pl. Ⅰ :4). At shedding stage, pollen grains are 3 - celled (pl. Ⅰ :5).

2.2 Ovule

The ovules are anatropous, crassinucellate and bitegmic (the growth of outer integument on the funicular side is arrested). Both integuments are 2 - layered. The micropyle is organized by the inner integument alone. At the megaspore mother cell stage, a group of funicular cells at the base of funicule become papillose, grow in the direction of the micropyle, and form an obturator that covers the outer opening of the micropyle later (pl.1:7).

2.3 Megasporegenesis and Female Gametophyte

A single hypodermal archesporial cell is differentiated in the ovular primordium. It divides transversely to form a primary parietal cell and a sporogenous cell (pl. Ⅰ:6). The sporogenous cell enlarges and functions as the megaspore mother cell (pl. Ⅰ:7). The megaspore mother cell divides meiotically and forms a linear tetrad of megaspore. The two megaspores in middle part degenerate sooner. The chalazal one and the micropylar one increase in size (pl. Ⅰ:8), the latter also degenerate afterwards. The chalazal megaspore is functional (pl. Ⅰ:9). It undergoes three successive mitoses forming 2 – , 4 – and 8 – nucleate embryo sac of the Polygonum type (pl. Ⅱ:1 ~ 2). The polar nuclei fuse and form the secondary nucleus (pl. Ⅱ:2). The antipodal cells degenerate at mature embryo sac stage (pl. Ⅱ: 2).

2.4 Endosperm

Endosperm formation is of the nuclear type. The primary endosperm nucleus divides earlier than the zygote (pl. Ⅱ: 3). Endosperm nuclei undergo free – nuclear division till the 12 – celled proembryo stage and the number of endosperm nuclei are up to more than 100 (pl. Ⅱ: 5). Then, the wall formation of the endosperm cells begins (pl. Ⅱ: 9).

2.5 Embryogeny

The zygote divides transversely and forms a terminal and a basal cell (pl. Ⅱ:4). The basal one divides transversely and then the terminal one divides vertically forming a T – shaped proembryo tetrad. The two juxtaposed cells derived from terminal cell divide vertically once again forming a quadrant (pl. Ⅱ:6 ~ 7). Meanwhile, the upper one of the two cells derived from basal cell divides vertically and the lower one divides transversely. At this time, the proembryo is 8 – celled. Then, the quadrant divide periclinally forming 4 dermatogen initials and 4 central cells (pl. Ⅱ:8). Thus, the embryogeny is of Juncus – variation of the Onagrad type (Johansen, 1950; Makde & Bhuskute, 1987).

3 Discussion

Generally, the genus *Kobresia* shares the embryological characters with these of the family Cyperaceae (Table 1). The pseudomonad pollen grains, the anatropous ovule, the *Polygonum* type of embryo sac formation and the *Onagrad* type embryogeny are all common in the family (Johri *et al* , 1992; Makde & Bhuskute, 1987; Dahgren *et al* , 1985; Nijalingappa, 1986). The situation, that the chalazal and micropylar megaspore of tetrad enlarge in size, the middle two degenerate earlier and then the micropylar one also degenerate, and the chalazal one becomes functional, is observed in the Cyperaceae for the first time.

Gilly (1952) once raised *Kobresia* and related genera (*Carex*, *Schoenoxiphium* and *Uncinia*) to a separate family, Kobresiaceae. The treatment is not supported by embryological evidence. “Pollen grains in pseudomonads, consisting of tetrads in which three microspores have degenerated and only one pollen comes to development" is one of the most important diagnostic characters of the family Cyperaceae (Dahgren *et al*, 1985). It is also the character of *Kobresia*. Other embryological characters are also agreeable to those of the family as stated before. Gilly (1952) considered that the tribe Cariceae was more closely related to the Poaceae than to other tribes of the Cyperaceae in respect of morphology. Nevertheless, the pollen arrangement at release, the ovule type, the integuments, the antipodals, and the embryogeny of *Kobresia* are different from those of the Poaceae, but the same as those of the Cyperaceae (Table 1). This suggests a relatively remote relationship between *Kobresia* and Poaceae. Embryologically, *Kobresia* should be a member of the family Cyperaceae, and the tribe Cariceae should be included in the family.

Table 1 Comparison of embryological characters of *Kobresia* with Cyperaceae, Juncaceae and Poaceae*

Characters	*Kobresia*	Cyperaceae	Juncaceae	Poaceae
Microsporogenesis	?	Simultaneous	Simultaneous	Successive
Pollen arrangement at release	Pseudomonad	Pseudomonad	Tetrahedral, tetragonal, Isobilateral, Rhomboidal tetrad	Monads
Ovule type	Anatropous	Anatropous	Anatropous	Ana-, hemiana-, or campylotropous
Outer integument on funicular side	Undeveloped	Undeveloped	Developed	Developed
Embryo sac	*Polygonum*	*Polygonum*	*Polygonum*	*Polygonum*
Antipodals	Ephemeral	Ephemeral	Ephemeral	Persistant
Endosperm formation	Nuclear	Nuclear	Helobial	Nuclear
Embryogeny	Onagrad, *Juncus* - variation	Onagrad, *Juncus* - variation	Onagrad, *Juncus* - variation	Asterad

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References

Bruhl J, 1995. Sedge genera of the world: relationships and a new classification of the Cyperaceae [J]. *Austr Syst Bot*, **8** (2): 125~305

Dahgren R M T, Clifford H T, Yeo P T, 1985. The Families of the Monocotyledons [M]. Berlin: Springer-Verlag

Gilly C L, 1952. Phylogenetic development of the inflorescence and generic relationships in the Kobresiaceae [J]. *Iowa State Coll J Sci*, **26**: 210~212

Johansen D A, 1950. Plant Embryology [M]. Waltham, Massachusetts: Chronica Botanica Comp.

Johri B M, Ambegaokar K B, Srivastava P S, 1992. Comparative Embryology of Angiosperms [M]. Vol. 2. Berlin: Springer-Verlag

Kirpes C C, Clarke L G, Lersten N R, 1996. Systematic significance of pollen arrangement in microsporangia of Poaceae and Cyperaceae: review and observations on representative taxa [J]. *Amer J Bot*, **83** (12): 1609~1622

Linder H P, Kellogg E A, 1995. Phylogenetic patterns in the Commelinid clade. In: Rudall P J, Cribb P J, Cutler D F, *et al*, eds.

Monocotyledons: systematics and evolution [M]. Kew: Royal Botanic Gardens, 473 ~ 496

Makde K H, Bhuskute S M, 1987. Embryology of *Kyllinga monocephala* (Cyperaceae) and its systematic position [J]. *Pl Syst Evol*, **156**: 143 ~ 150

Metcalf C R, 1971. Anatomy of the Monocotyledons. V. Cyperaceae [M]. Oxford: Claredon Press

Muasya A M, Simpson D A, Chase M W, Culham A, 1998. An assessment of suprageneric phylogeny in Cyperaceae using *rbc*L DNA sequences [J]. *Pl Syst Evol*, **211**: 257 ~ 271

Munro S L, Linder H P, 1997. The embryology and systematic relationshipsof *Prionium serratum* (Juncaceae: Juncales) [J]. *Amer J Bot*, **84** (6): 850 ~ 860

Nijalingappa B H M, 1986. Embryology of *Scleria foliosa* (Cyperaceae) [J]. *Pl Syst Evol*, **152**: 219 ~ 230

Padhye M D, Makde K H, 1982. Embryogeny in some Cyperaceae [J]. *Pl Syst Evol*, **139**: 279 ~ 287

Explanation of Plates

Plate Ⅰ 1 – 5. Anther and microsporogenesis of *Kobresia filicina*. 1: TS anther with 4 sporangia, × 480; 2: TS anther at early 2 – nucleate stage showing vestigial degenerated microspores, x1200; 3: TS anther showing 2 – nucleate pollen grains, vestigial degenerated microspores and spiral thickening of endothecium, × 1200; 4: LS anther showing 2 – nucleate pollen grains, × 1200; 5: TS anther at shedding stage showing 3 – celled pollen grain and papillose epidermis of anther wall, × 1200. 6 – 9. Megasporogenesis and megagametogenesis of *Kobresia filicina*. 6: LS ovule showing sporogenous cell, × 1200; 7: LS ovule showing megaspore mother cell, × 768; 8: LS ovule showing tetrad of megaspore and enlarged chalazal and micropylar megaspores, × 1200; 9: LS ovule showing functional megaspore, × 1200.

Plate Ⅱ 1 – 2. Megagametogenesis of *Kobresia filicina*. 1: LS ovule showing 2 – nucleate embryo sac, × 1200; 2: LS ovule showing mature embryo sac, the secondary nucleus, the egg cell and one synergid can be seen, × 1200. 3 – 9. Embryogeny and endosperm formation of *Kobresia curvata*. 3: LS ovule showing zygote and endosperm nuclei, x1200; 4: 2 – celled proembryo, × 1200; 5: Early proembryo and endosperm nuclei, × 1200; 6: 5 – celled proembryo, and one cell at the chalazal end is undergoing mitosis, × 1200; 7. Proembryo between 8 – to 12 – celled stages, × 1200; 8: 14 – celled proembryo, × 1200; 9: 14 – celled proembryo and endosperm cells, × 192.

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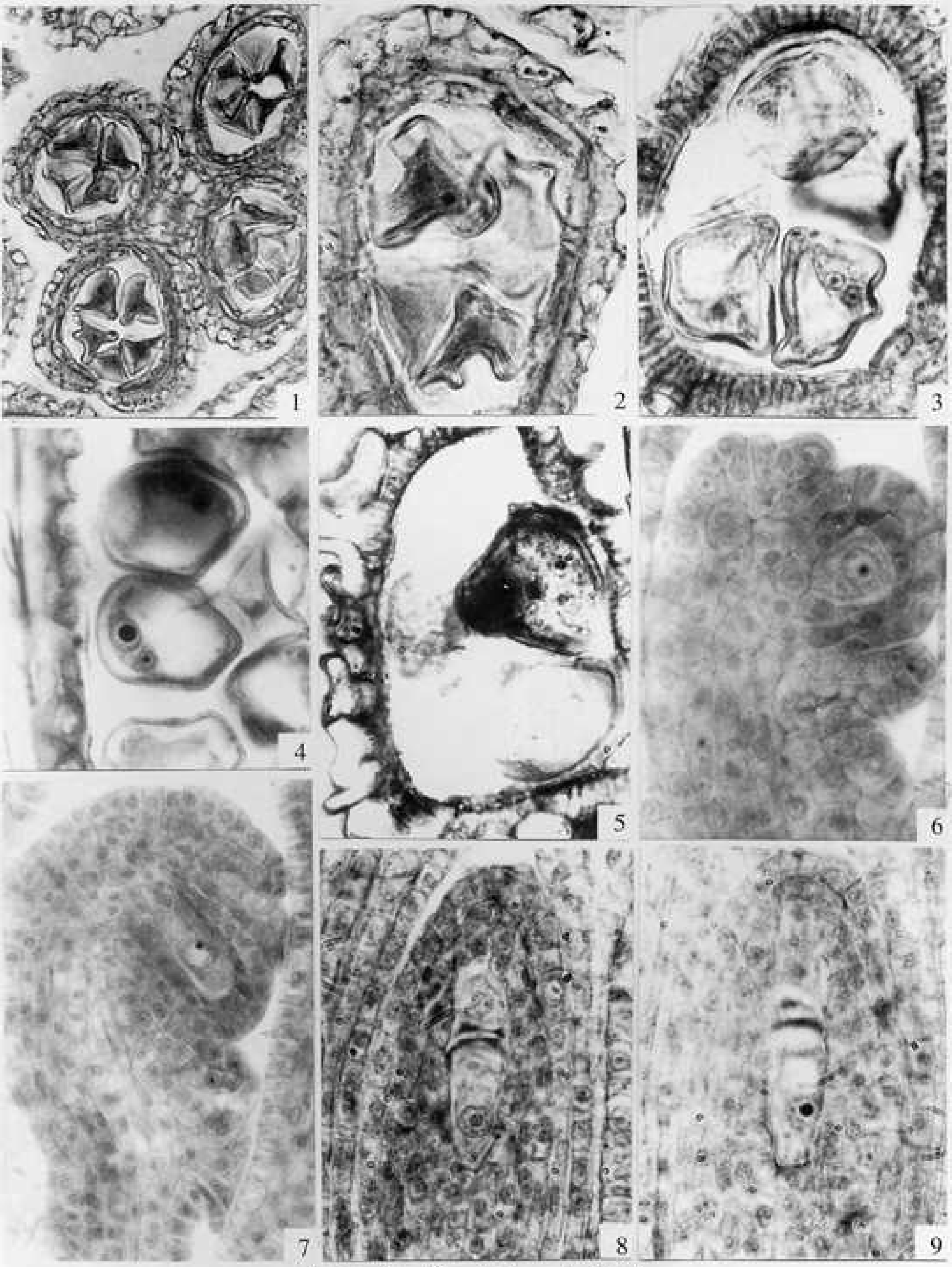
Plate Ⅰ 1. cross section of the anther, showing tapetal cells and microsporocyte. × 3000; 2. two nuclei of tapetal cell in a state of mosaic. × 10000; 3. plastids changes in shape. × 15000; 4. wall of tapetal cell, endoplasmic reticulum, plasmodesma. × 30000; 5 ~ 7. course of plastid membrane invagination. × 30000; 8. multiple membranes body in the vesicle. × 20000; 9. endoplasmic reticulum in astate of concentric range. × 15000; 10. expansion of endoplasmic reticulum. × 20000.

Plate Ⅱ 11. expansive endoplasmic reticulum and Golgi apparatus. × 40000; 12. plasmalemma invagination (arrow). × 15000; 13. wall of tapetal cells dissociates and disappears, the amorphous materials in the plasmalemma invagination (arrow) is released to microsporangium. × 15000; 14. plasmalemma invagination (arrow). × 20000; 15. wall of tapetal cells dissociates. × 15000; 16. the plasmodesmata will be broken down. × 20000; 17. plasmalemma (arrow). × 60000; 18. showing the microspore and the wall materials (o) in the microsporangium; 19. the wall materials (o) are located in the place of cell wall dissociated. × 35000; 20. tapetal cells and the tetrad. × 5000.



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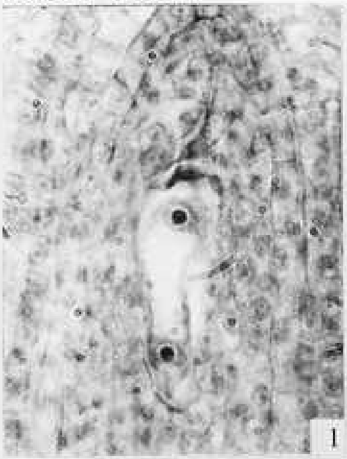
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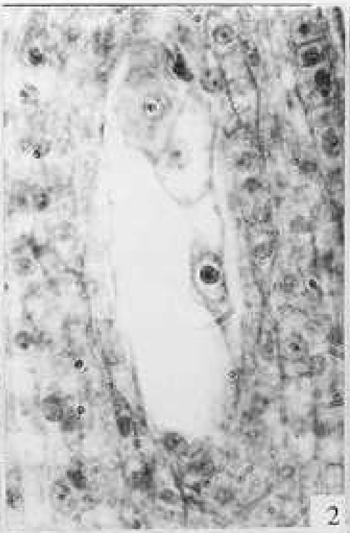
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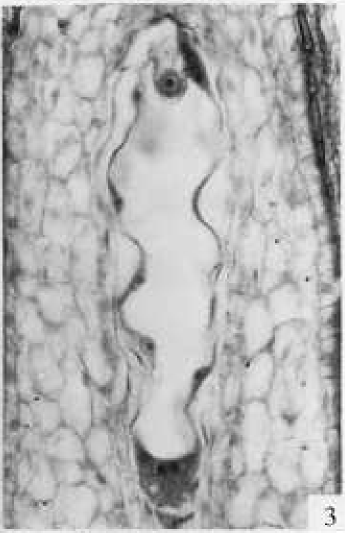
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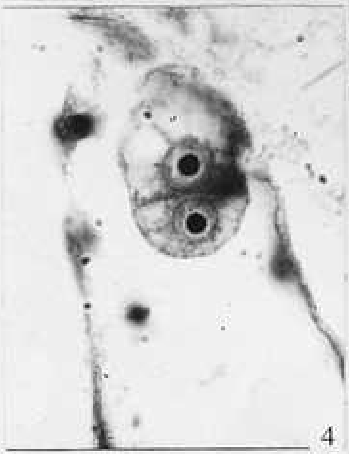
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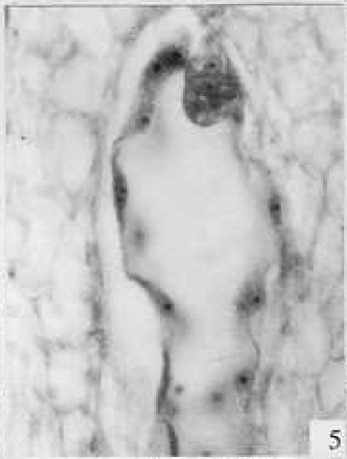
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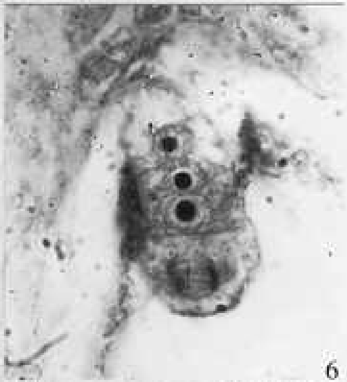
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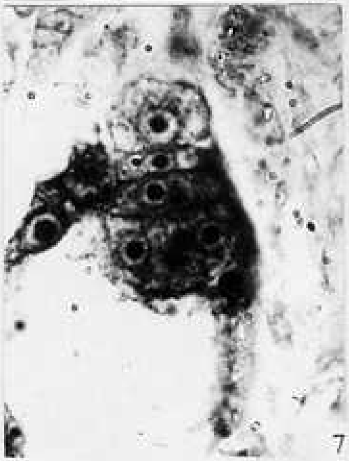
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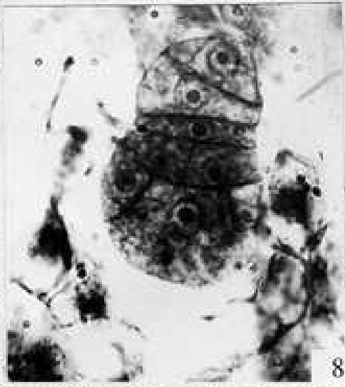
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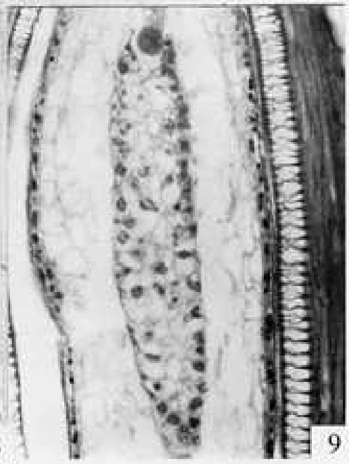
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